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The Development of the Trigeminal Nerve  
of the Chick with Special Reference to the  
Maxillary Division & its Peripheral Ganglia

Zoology

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THE DEVELOPMENT OF THE TRIGEMINAL NERVE OF  
THE CHICK WITH SPECIAL REFERENCE TO THE  
MAXILLARY DIVISION AND ITS  
PERIPHERAL GANGLIA

BY

GERTRUDE AMELIA JOHNSON  
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IN

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

*Gertrude Amelia Johnson*

ENTITLED *The Development of the Trigeminal Nerve  
of the Chick with Special Reference to the  
Maxillary Division and its Peripheral Ganglia*

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

DEGREE OF *Master of Arts*

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on

Final Examination





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## I. INTRODUCTION

Although various investigators have worked on the development of the different cranial nerves and the cerebro-spinal ganglia in all groups of vertebrates, they have apparently given very little attention to the development of the cranial sympathetic system. At any rate the literature on this subject is meagre. The ganglia of the system in question are small and the boundaries of some are very difficult to determine, since they are made up of several little scattered groups of nerve cells. For example, Müller and Dahl (1910, p. 73) make the following statement with regard to the sphenopalatine ganglion in man:- "Der grund für die ausserordentlich schwierige Darstellung des Gangl. sphenopalatinum liegt nicht nur in seiner versteckten Lage, sondern vielmehr noch darin, dass dieses Ganglion so sehr klein ist und augenscheinlich manchmal noch in einzelne Teile zerfällt, die dann die Grenze der Sichtbarkeit kaum überschreiten." It rather pleased me to find this statement, since the conditions, as I found them in the case of the sphenopalatine ganglion of the adult fowl, corroborate such a description. Müller and Dahl also found the ciliary and sub-maxillary ganglia to be more or less scattered.

The majority of these cranial peripheral ganglia do not begin to develop until rather late; that is, after several branches and communicating rami have developed on most of the cranial nerves, so that there is quite a complex of well developed nerves and groups of loosely associated fibers. It is





evident, that with such an intermingling of nervous tissue through rami and anastomoses, one must meet with difficulties in trying to trace apparently separated peripheral groups of neuroblasts back to the nerve to which they belong. This is especially true, if, as in the case of the chick embryo, the ganglia, in their earliest stages of development, are considerably more in evidence than their weak and sometimes practically lacking fibrous connections.

Since, in the adult vertebrates, there are so many rami and anastomoses by means of which the nerves of the head are connected with one another, directly or indirectly, the origin of the peripheral ganglia might be attributed to any one of several cerebro-spinal ganglia, or to cells which have migrated along the ventral roots of these same nerves. Perhaps the most reliable means, therefore, of determining somewhat accurately the origin of the ganglia, is through a study of the embryonic development of the cerebro-spinal ganglia and nerves most intimately associated with the peripheral ganglion in question. For this purpose I chose the chick embryo for two reasons; first, I could get any stage desired by merely taking the eggs out of the incubator and killing the embryo immediately in some fixing fluid: second, I avoided the difficulty of raising embryonic material in a laboratory with varied temperatures.

This work was done in the Zoological laboratory of the University of Illinois under the guidance of Professor F. W. Carpenter. It is with pleasure that I acknowledge my indebtedness to Professor Carpenter for his unfailing interest and helpful suggestions all through this work.



## II. DESCRIPTION OF THE SPHENOPALATINE GANGLION IN THE ADULT FOWL

The sphenopalatine ganglion, as is well known, belongs to the group of cranial autonomic ganglia. Its connections with the maxillary and ophthalmic branches of the trigeminal nerve and with the facial nerve vary somewhat with the different classes of vertebrates. In some vertebrates, as the fishes and probably the amphibians, it does not exist. In birds and mammals it has been found to be connected with the tear gland and mucous glands of the nasal cavity on the one hand, and with a branch of the facial nerve on the other. In birds, according to H. Gadow (1891), it is connected with the inferior branch of the facial nerve by a very short ramus, and with the tear gland, by means of a fine ramus to the nasal branch of the trigeminus. Those fibres destined to penetrate the mucous membrane of the nasal cavity probably turn after uniting with the nasal branch and enter the olfactory opening along with this nerve. Several branches of the maxillary nerve are described by Elizabeth Cords (1904), and in connection with one of these branches she mentions the sphenopalatine ganglion, saying that it is of microscopic size. A diagrammatic representation, in the article by Müller and Dahl (1910), of the cranial nerves in man, shows the following connections for the sphenopalatine ganglion. Some neurones, which have their origin in this ganglion, pass by way of a short ramus to the maxillary nerve, whence they go over to the zygomatic nerve. They run along this nerve until they reach the temporal ramus; here they turn and pass up





the ramus to the lacrymal branch of the ophthalmic nerve. They then bend again, and along with the lacrymal branch end in the tear gland. Two nerves, according to the above diagram, the posterior nasal ramus and probably the anterior nasal ramus, emerge directly from the sphenopalatine ganglion and penetrate the mucous membrane of the nasal cavity. Along these nerves the autonomic fibres from the sphenopalatine ganglion take their course. The ganglion is connected with the facial nerve by the major superficial petrosal branch of that nerve.

Müller and Dahl (1910) believe that the nerve fibres, which go from the sphenopalatine ganglion to the tear gland, control the responses to emotions which cause weeping, while fibres, from the spinal sympathetic system, control the reflex secretions of the gland. They put forth a similar argument with regard to the nerves coming from this ganglion, which are connected with the olfactory organ. Thus, in the case of some people, embarrassment will produce an effect similar to the sudden acquisition of a cold. That the neurones in the sphenopalatine ganglion are of a sympathetic nature, at least as far as their structure is concerned, has been shown by Carpenter (1912), who studied the cranial autonomic ganglia of the sheep. The same is true, however, for the horse and other mammalia (Müller and Dahl, 1910). It therefore seems very probable, that if the peripheral ganglia of the head of an adult bird were examined for such structures as would indicate the nature of the cells therein, the neurones would show a sympathetic structure, since the relations are similar to those in mammals.



In the adult fowl, the sphenopaltine ganglion is barely recognizable as an enlargement on the maxillary nerve; and its connections with other nerves than the maxillary are difficult to work out, because the rami are so fine and often penetrate cartilaginous or bony substances. It is situated about 0.5 mm. back of the internal nasal opening in the floor of the eye socket. At this point it is connected with a branch from the facial nerve and probably by a ramus to the tear gland. A part of the maxillary nerve was cut out at this juncture and fixed in Bouin's fluid. It was stained in Delafield's haematoxylin. By this means I was able only to distinguish the nerve cells from the supporting cells. The former were large and darkly stained, and were scattered here and there among the fibres in groups of various sizes. Had I cut out a larger piece of the maxillary nerve in that same region, I would probably have found some more stray nerve cells.





### III. DEVELOPMENT OF THE MAXILLARY DIVISION OF THE TRIGEMINUS AND ITS PERIPHERAL GANGLIA.

#### A. Historical Survey.

Literature on the development of the sphenopalatine ganglion, as has been previously stated, is very meagre in spite of the fact that several investigators have worked on the development of the trigeminal and related cranial nerves.

The earliest appearance of the fundment of the trigeminus of the chick has been observed in an embryo of about forty-five hours' incubation, (10-20s), (Lillie, 1908). In birds, two roots of the trigeminus, a motor and a sensory, have been described. In mammals, the nerve not only has a motor as well as a sensory root, but it has a separate motor branch, which on leaving the ganglion appears as one of two distinct components of the mandibular nerve, but later separates and forms an independent branch (Belogowy, 1910). Belogowy also found, while making observations on pig embryos, three divisions of the Gasserian ganglion, a mesocephalic, a maxillary and a mandibular. The maxillary division was, however, more intimately associated with the mandibular than with the mesocephalic division. In man also, three divisions have been observed in the developing Gasserian ganglion (Giglio, 1902). Thus, instead of the maxillary nerve being only indirectly connected with the Gasserian ganglion as a branch of the maxillo-mandibular division of the trigeminal nerve, which is true in the case of birds (Belogowy, 1910 ).



it enters the maxillary division of the ganglion directly.

The different rami connected with the trigeminal nerve and its peripheral ganglia in the adult birds and mammals have been described by several investigators, but these descriptions of course give us very little clue as to the origin of these autonomic ganglia. According to the observations of Remak (1851) on chick embryos and of Kölliker (1879) on rabbit embryos, the ciliary, sphenopalatine and otic ganglia are derived from cells which have become separated from the Gasserian ganglion. Rubasckin<sup>h</sup> (1897) describes a transitory ganglion on the olfactory ramus of the ophthalmic branch, which he calls the olfactory ganglion. Carpenter (1906), while making a study of the development of the ciliary ganglion and the oculomotor and abducent nerves, and Kuntz (1913), while working on the development of the autonomic ganglia of the pig, found only a part of the ciliary ganglion to be derived from cells which had migrated along a ramus communicans of the ophthalmic branch of the trigeminus to the above named ganglion. Its remaining cells have their source in the floor of the mid-brain. Kuntz also found the neuroblasts composing the sphenopal<sup>a</sup>atine ganglion on the maxillary branch, and some neuroblasts composing the otic and submaxillary ganglia on the mandibular branch to be derived from cells which had migrated along the nerve fibres from the Gasserian ganglion. In addition, the otic and submaxillary ganglia receive cells from the wall of the hind-brain. In its earliest stages of development the sphenopalatine ganglion is more proximal in position than later (Kuntz. 1913). He does not make a definite state-





ment as to whether these nervous elements wander as indifferent cells, or as young neuroblasts to the various places where the peripheral ganglia develop.

## B. Observations.

I. Method. Since the chick embryos used for this investigation represented rather late stages, only the heads were sectioned except in the case of the two youngest embryos studied. Serial sections of these two stages, one ninety-four hours old, the other one hundred and nineteen hours old, were loaned to me for use in this work by Dr. F. W. Carpenter. For the method of preparation see Carpenter (1906, p. 175).

The embryos used for a study of the later stages were fixed entire in a mixture of corrosive sublimate and acetic acid. The heads were not removed from the bodies until they were ready to be placed in 100% alcohol, the bodies being left in 95% alcohol for possible future use. All the heads were infiltrated and imbedded in paraffin. It was not found necessary to decalcify. The sections were cut twelve to fifteen micra thick according to the age of the embryo, and stained in Heidenhain's iron haematoxilin. A rather pale stain was found to be the best for my purposes, since it brought out the ganglion cells and nerve fibres in rather sharp contrast to the other differentiated cell groups and the mesenchyme.

Serial sections of the embryos were cut in the two following planes:

a. Sagittal. Since the op<sup>h</sup>thalmic branch of the



trigeminal nerve extends in an antero-ventro-median direction, and the maxillary nerve almost directly ventro-laterad, the sections cut most of the trigeminal nerve more or less obliquely, except along the more median maxillary branch, in which there is a broad bend directly ventrad from a point near the proximal end to a point a short distance from the distal end, when it turns mediad. Both the more median and the more lateral maxillaries turn almost directly mediad near their distal ends, so that in both cases, starting from the median plane, a series of cross sections could be seen before any other parts of the branches were reached. The above appearance of the maxillary branches is especially characteristic of the embryo representing the fourth stage in the development of the trigeminal nerve. In the stages younger than this the more lateral maxillary branch is lacking, while in the older stages it is comparatively weaker and has one or two long proximal branches.

b. Transverse. These were hardly true cross sections since they were cut at an angle between frontal and cross sections, as nearly horizontally through the mid-brain as could be estimated, in order to get some sections through as full a length of the maxillary branches as possible. None of these sections was studied as thoroughly as the sagittal, since the latter brought out to a better advantage the relationships of the trigeminal to other cranial nerves and to structures more or less intimately connected with it.





2. Description of the development of the trigeminal nerve. The description of the earliest development of the trigeminal nerve, here given, will be based upon Lillie's textbook, "The Development of the Chick". The remaining stages, beginning with a chick embryo of ninety-four hours' incubation, will be described from direct observations.

a. Stage I. According to Lillie the neural crest originates from the most dorsal cells of the medullary plate and from the ectoderm immediately adjacent. There are at least three kinds of cells found in the neural crest, viz., those forming mesenchyme cells, those forming neuroblasts and those forming sheath cells. In the head region, the neural crest may be divided into pre- and post-otic divisions, which arise at different times. Goronowitsch divides the pre-otic part of the cranial neural crest into primary and secondary ganglionic crests. According to him there is a decided difference in the time of origin of the two, the primary, which includes the region of the fore- and mid-brains, arising before the secondary, which includes the region of the trigeminus and acustico-facialis. Lillie, however, did not find such a difference in his preparations.

At the stage of 10s, the neural crest has lost its connection with neural tube. Behind the optic vesicles the cells of the neural crest spread out laterally, forming a periaxial layer between the ectoderm and axial layer of mesenchyme derived from the region of the fore-gut. Above the mandibular and hyoid arches at slightly later stages, the periaxial layer condenses and thickens, forming strong cords which are the primordia of the



trigeminus and acustico-facialis ganglia, and mark the paths of the trigeminal and facial nerves. Both cords are attached to the hind-brain, the trigeminus in the first neuromere of the myelencephalon, the acustico-facialis in the third. They are supplemented by proliferations of the ectoderm on each side of the first visceral pouch. The trigeminal cord enters the mandibular arch, the facial, the hyoid arch, and in the stages between 20 and 30 somites they form at least part of the mesenchyme of these arches. The ganglia differentiate from the upper portions of the cords. The trigeminus divides over the angle of the mouth and sends out an extension into the rudimentary maxillary process: a third process of the cord forms the path of the ophthalmic division of the trigeminus. At the stage of about 27 s (seventy hours?) the trigeminus forms a connection with a thickening of the ectoderm (placode of the trigeminus) situated in front of and above the first visceral cleft: the acustico-facialis connects in a similar manner with a layer of ectodermal thickening (placode of the facialis) situated on the posterior margin of the uppermost part of the first visceral furrow. These ectodermal thickenings represent parts of the sensory canal system of the heads of aquatic vertebrates and are therefore only rudimentary structures of brief duration. At the seventy-two hour stage there are two ectodermal thickenings in connection with the trigeminus, one in front of the other, and probably derived by division of the original. The facialis placode is not divided, but is more fully developed.

b. Stage II. This stage is represented by a series of transverse sections of a chick embryo of ninety-four hours' incubation.





At this stage the Gasserian ganglion shows two divisions very distinctly, a mesocephalic and a maxillo-mandibular. It extends almost directly in a postero-anterior direction, being only slightly oblique in position, so that the maxillo-mandibular division is a little more lateral in position than the mesocephalic. The nerves, the ophthalmic and the maxillo-mandibular, coming from these two divisions of the ganglion, are unbranched. The ophthalmic branch passes straight cephalad from the mesocephalic division of the ganglion along the lateral wall of the anterior cardinal vein and terminates dorsad of the optic stalk between the fore-brain and the eye-ball just caudad of the laterally projecting hemisphere of that side (Carpenter, 1906). The maxillo-mandibular branch emerges from the median surface of the maxillo-mandibular division of the ganglion, opposite a point somewhat ventral to the center of this division. It extends in a slightly antero-ventral direction, passing along the lateral surfaces of the anterior cardinal vein and the aortic arch and terminating in the mandibular arch at a point a short distance ventral to the pharynx. All along the nerve, scattered among the fibres, are found indifferent cells which have probably migrated from the Gasserian ganglion, and which are very likely destined to become neuroblasts or cells of the sheath of Schwann. As soon as the nerve passes the ventral boundary of the ganglion, it becomes surrounded by a dense mass of mesenchyme cells which have assumed a more or less rounded form. When some of the later stages are considered along with this series, it seems quite evident that this group of cells is the anlage of a muscle, although





it is not so clear at this time, since the cells have not as yet assumed the characteristics which differentiate developing muscle cells from mesodermal cells in other groups which may be the anlagen of other tissues. It is very possible, too, that those cells immediately surrounding the nerve take part in the formation of a connective tissue sheath around the future nerve.

From the appearances shown by the grouping of these cells, four rather interesting questions are brought to one's mind. Did this group of cells influence the path of the nerve? Did the presence of the nerve stimulate the mesenchyme cells in that vicinity to group themselves toward the formation of the anlage of a muscle? Did neither influence the other? Was the stimulus mutual and due to the relative position of one to the other or of both to the anlage of some other organ or system? Arguments might be gathered in favor of any of the above views. If a group of cells had not formed as an anlage of a muscle what would have determined the direction of the nerve? Nerve branches are known to develop and later degenerate if they do not penetrate, or end in the tissue for which they are destined. The fundamentals of some organs and muscles are formed before they are penetrated by any part of a nerve. The stage of development of the nervous system during early embryonic growth especially, is considerably in advance of other systems. The nervous system in all stages of development, including the adult, is the most influential and highly complex system, and the most important factor in controlling all life activities, voluntary or involuntary. Many other facts could be innumrated which would bring the weight of evidence more



favorably toward one view or another, but to me the second or fourth of the above views seems the most probable; that is, either the presence of the nerve influenced the formation of the muscle anlage, or the stimulus was mutual. I am inclined to favor the former for at least the larger nerves formed very early in the development of the chick and directly connected with the central nervous system, and the latter, for the branches not directly connected with, or at a greater distance from the central nervous system.

c. Stage III. An examination of sagittal sections of a chick embryo of one hundred and nineteen and one-half hours' incubation was made for this stage of development of the trigeminal nerve.

A strong ophthalmic branch extends completely around the anterior half of the eye along the median surface (Pl. I, Fig. 1, rm. oph.). The mandibular branch is stout but is still quite short and extends in a postero-ventral direction into the mandibular arch (Fig. 1, rm. md.). There is a weak maxillary branch given off from the proximal end of the maxillo-mandibular division, which extends in an antero-ventral direction toward the dorso-posterior surface of the eye (Fig. 1, rm, mx.). Along all of the branches and more or less evenly distributed among the fibres are indifferent cells, many of which show various stages of mitotic division. None of the primary divisions of the trigeminal nerve are branched at this stage, but a slight, yet unquestionable connection between the ophthalmic branch of the trigeminus and the root of the oculomotor nerve was observed.





d. Stage IV. A Study of serial sections of the head of a chick embryo of about seven days and five hours' incubation was made for the fourth stage of development of the trigeminal nerve. One half of the head was cut in sagittal sections. The other half was cut in a plane at an angle between a true cross section and a frontal section, such that the plane of the sections was parallel to the long axis of the mandibles.

The mesocephalic ganglion and its nerve, the ophthalmic, were not studied in detail at this stage. The mandibular branch, which at this time connects directly with the maxillo-mandibular division of the Gasserian ganglion, arises as two nerves, one from the median surface of the ganglion and the other from the lateral. These nerves meet at a point slightly ventral to the peripheral end of the ganglion to form a single nerve, for a short distance only, since the mandibular nerve at this stage soon splits up into several branches. Some of the most important and most interesting of these are shown in Pl.I, Fig.2, 1, 2, 3, . One branch of considerable interest is more lateral in position than the rest. It crosses over into the upper mandible and passes along the posterior surface of the infrapalatine vein(?), ending near the ectal surface of the mandible (Fig.2,1.). Another branch, given off at a point just ventrad to the ventro-lateral surface of Meckel's cartilage, passes along the postero-ventral surface of this cartilage for some distance, then turns in a ventral direction, ending close to the ectal surface of the lower mandible (Fig. 2, 3.).



The maxillary division emerges as three main branches from the peripheral end of the maxillo-mandibular division of the Gasserian ganglion, and these break up into several smaller rami along the lateral surface of the ganglion. The most anterior of these is very short and extremely lateral in position. It extends in an antero-ventral direction, passing directly into the external rectus muscle of the eye where it anastomoses with the sixth nerve (Fig. 2, rm. mu. rt, e. ). The branch just posterior to this is the most median in position and passes along the posterior surface of the eye ending near the nasal cavity (Fig. 2, I). The third branch is very lateral in position and extends in a ventral direction, passing along the antero-lateral surface of the infrapalatine vein (?), beyond which it divides into two unequal branches. The stouter of these still continues in a ventral direction toward the ectal surface of the upper mandible, while the other turns in a postero-ventral direction, ending just at the posterior margin of the mandible (Fig. 2, II a, II b). Up to this time I have found no indication of a ganglion along any of the branches of the maxillary nerve.

e. Stage V. An embryo of about nine days' incubation was used for this stage. Only sagittal sections were cut from one half of the head of this embryo. The other half was not sectioned.

At this stage the orientation of the Gasserian ganglion has changed considerably. Instead of extending almost in an antero-posterior direction, it has turned to an angle of about  $45^{\circ}$  from the median plane so that the maxillo-mandibular





division is much more lateral in position than the mesocephalic. The ophthalmic branch will not be described in detail for this stage nor for any of the following stages. Two nerves originate from the maxillo-mandibular division of the Gasserian ganglion at this stage. One emerges from the ganglion along its median surface, while the other emerges along its lateral surface. The nerve given off from the median surface is probably that part of the maxillo-mandibular division including the mandibular nerve and one branch of the maxillary. The nerve given off from the lateral surface is another branch of the maxillary.

As the more median division of the maxillo-mandibular nerve emerges from the antero-ventral end of the ganglion, it extends in an antero-ventral direction for a short distance, after which it turns ventrally, passing along the anterior surface of the quadrate bone. Just after reaching the dorso-anterior angle of the above named bone the mandibular nerve divides. One branch extends in a more or less direct medio-ventral direction, ending at the antero-ventral angle of Meckel's cartilage (Pl.I, Fig. 3, 1,). The other branch turns in a medio-posterior direction for a short distance. As it turns again a small branch is given off which ends in one of the larger muscles of the lower mandible. The main part of the branch gradually bends in a ventro-lateral and slightly anterior direction, passing between the dorso-anterior surface of the ventral part of Meckel's cartilage and the ventro-posterior surface of the supra-angular bone. When it reaches the ventro-anterior angle of Meckel's





in  
cartilage it turns, a median direction, reaching almost the median plane of the head, and ending near the ectal surface of the lower mandible (Fig. 3, 2,). About mid-way along the dorso-anterior surface of the distal half of Meckel's cartilage, a short branch is given off from the nerve which extends slightly medially and ventrally. Along the full length of this branch is a ganglionic mass, which is probably the anlage of the sub-maxillary ganglion of the adult fowl (Fig. 3, gn. md. ). This ganglion as the above description shows is very median in position.

The maxillary branch is given off at a point a little ventral to the antero-ventral surface of the quadrate bone. Its course gradually changes from a ventral to a more or less antero-ventral one. Practically all of this branch, with the exception of a very proximal portion, is comparatively very median in position. At a point about midway between the postero-ventral surface of the eye socket and the dorsal surface of the supra-angular bone it divides into two branches, one being more posterior and lateral in position than the other (Pl. I, Fig. 3, I, II.). On both branches were found scattered ganglionic masses, many of which apparently had no connection with any other; that is to say, all indications of young neuroblasts disappeared in several consecutive sections, and reappeared again in a more ventral or dorsal position than the ganglionic mass previously observed (Fig. 3, gn. mx.). Some of the ganglionic masses on the more median maxillary branch are right in line antero-posteriorly with the ganglion found at the peripheral end of the more median mandibular branch.



The neuroblasts composing these peripheral ganglia are much smaller than those found in the Gasserian ganglion (Pl. II. Fig. 9, cl. gn. mx. ). No neuroblasts were observed along the nerve between these ganglionic masses and the Gasserian ganglion. This excludes the possibility that these cells were derived from the Gasserian ganglion as young neuroblasts. The most plausible explanation, therefore, seems to be that the indifferent cells which are found along the entire length of the nerve and have migrated from the Gasserian ganglion or the ventral root of the trigeminal nerve, have accumulated in masses here and there along the distal half of the nerve, and then developed into young neuroblasts. This becomes even more apparent when it is seen that these scattered accumulations of neuroblasts are composed of cells which vary greatly in size and consequently in stages of development (Pl. II, Fig. 7). Since the sphenopalatine ganglion in the adult fowl is a rather scattered ganglion, these scattered and apparently separate ganglia are probably the anlage of the sphenopalatine. Although I have not been able to trace the fate of this group of ganglia far enough at present to make a positive statement as to whether or not this is, in reality, the sphenopalatine ganglion, yet the fact that there is a group of ganglia on the maxillary nerve and a well defined peripheral ganglion on the mandibular nerve seems to be pretty strong proof that this is the sphenopalatine.

That division of the maxillary nerve which comes from the lateral surface of the Gasserian ganglion divides into two branches a short distance from the proximal end. The more





lateral branch is about three-fourths as long as the more median one. Both branches turn from a more or less postero-ventral direction to an antero-ventral one, passing around the postero-ventral surface of the eye. The longer branch extends a little beyond a point opposite the center of the eye on the postero-ventral surface (Pl. I. Fig. 3, mx. orb. 1 ). The more lateral branch gives off a small ramus near its peripheral end, which in its turn branches so as to form a sort of net-work of very fine nerves (Fig. 3, mx. orb. 2 ). These two branches of the maxillary nerve are extremely lateral in position and are probably part of that division of the nerve, which, in the adult, gives off branches to the Harderian gland, the conjunctiva of the eye, the nictitating membrane and the eye-lids. For convenience these nerves will hereafter be termed the orbital group.

f. Stage VI. The characteristics shown in the development of the trigeminal nerve at this stage are found in a chick embryo of eleven days and one hour's incubation. The observations were made on sagittal sections cut from one-half of the head of the embryo.

The Gasserian ganglion at this stage has assumed a rather flattened, crescent-shaped appearance, with its greatest width latero-mediad. In the previous stages the constriction between the two divisions of the ganglion was more marked than it is at this time.

A very interesting change has taken place between this stage and the one previously described, in the development



of the maxillo-mandibular nerve. That the full significance of this change may be understood, I shall give a short account of some observations made on a previous stage. Since my observations on this intermediate stage were very incomplete, due to the fact that only the more median sections (the sections were cut in a sagittal plane) were ready for study, I concluded that it was preferable to describe this stage in connection with the sixth. Close to the median plane of the head and in the upper mandible, part of a nerve was observed with a ganglionic mass in the region of the nasal cavity. The more lateral sections revealed the fact that there were several such ganglia scattered all along this nerve until it disappeared, apparently without connecting with any known cranial nerve or with any part of the brain. I tried to find a connection with some part of the brain or with a cerebro-spinal ganglion toward the median plane, but failed. Since the series included a few sections on the opposite side of the median plane, I was able to make the reconstruction shown in Plate II, Figure 5. From this figure it seems quite evident that there must be a similar nerve on the opposite side of the head.

The observations made on the embryo representing the last or sixth stage, show the following interesting facts.

Near the median plane of the upper mandible a part of the distal half of a nerve appears, along which are several scattered ganglionic masses (Pl. II, Fig. 6). This nerve is apparently not connected with any other nerve on the same





or opposite side of the head, nor with any part of the brain. The neuroblasts composing the ganglionic groups found along this nerve show signs of disintegration (Pl.II, Fig. 8, cl. gn. trans.). In a more lateral plane, also in the upper mandible, and close to the nasal cavity, another group of ganglia was observed. The ganglia included in this group are much larger and less scattered than those in the group previously described (Pl. I, Fig. 4, gn.sph.) They are on a branch of the maxillary nerve. This is made evident by the fact that the nerve can be traced into the maxillo-mandibular division of the Gasserian ganglion. It is very probable, therefore, that this group of ganglia makes up the sphenopalatine ganglion of the adult. Some of the neuroblasts from this group of ganglia are shown in Pl. II. Fig. 8, cl. gn. sph. .

With the above facts in mind and from the condition found in stage V (Pl.II. Fig. 5) what is the most plausible explanation of the meaning of those apparently disconnected nerves, with the groups of ganglia scattered along their course, found near the median plane in the upper mandible of the chick embryo? The following explanation seems to me to be the only plausible or possible one. The more median branch, shown in Plate I, Figure 3,1, at some stage developed a connection with a similar branch on the opposite side of the head; at a still later stage its connection with the trigeminal nerve was lost through disintegration; still later the connection between the two more median branches on the opposite sides of the head was lost, and the process of disintegration had then gone so far as to affect the neuroblasts composing the ganglia scattered along these nerves. The more lateral branches





in each case evidently found the more favorable courses and persisted as parts of the trigeminal nerves, while the ganglia found along them gradually grouped themselves together more and more to form the sphenopalatine ganglion.

The peripheral ganglion on the mandibular branch still persists, but shows no apparent increase in size. The nerves composing the orbital groups were rather hard to trace in this stage, but on some of the parts observed very small ganglia were found. The nerves are not very strong at best, and if they were torn a little in sectioning, or if the fixation had not been rapid enough, such parts of the nerves as would be necessary to understand their exact relationships, might easily have been torn or obscured in some way. The embryos were large and calcification of the bones had apparently at least begun.

### C. Discussion and Conclusion.

At the stage of five days' incubation, as has been shown, the trigeminal nerve has developed a long and strong ophthalmic branch, a short but stout mandibular branch and a very weak maxillary branch. A few hours after the seventh day of incubation both the maxillary and mandibular nerves have developed several rami. This seems to be generally true of all the cranial nerves which develop branches at any time. From observations of later stages it also appears that some of these rami are of a transitory nature. The peripheral expansion and extension of



nervous elements seems to have been unusually rapid at this time, because such a great difference was not found between any other two stages. At this stage, also, peripheral ganglia were observed on the facial nerve. Not until sometime between the eighth and ninth days of incubation, do peripheral ganglia appear upon the maxillary and mandibular branches. At this time two branches of the maxillary nerve present the appearance of a chain of ganglia linked together, in some cases by a few isolated neuroblasts and nerve fibres, and in other cases by nerve fibres alone. Young neuroblasts were not observed at any time migrating from the Gasserian ganglion along either the mandibular or the maxillary nerves. Thus it seems quite evident that these scattered accumulations of young neuroblasts must either have developed in situ or have migrated from some other cerebro-spinal ganglion. Since no connection between the trigeminus and the facial, or any other cranial nerve with a dorsal root ganglion or a ventral motor root could be found, neuroblasts of such an origin could reach the maxillary branch of the trigeminus only by migration through the mesenchyme. If such were the case, neuroblasts ought to have been seen in the mesenchyme between the region of these ganglia and such a nerve, probably the superficial petrosal branch of the facial. No such cells were observed. Another possible explanation still remains and it is the one which seems best to meet the conditions found here. At all stages numerous indifferent cells, some of which showed karyokinetic figures, were seen scattered among the fibres of both the mandibular and maxillary





branches. It therefore not only seems possible, but also very probable, that some of these indifferent cells were destined to develop into neuoblasts which would take part in the formation of some peripheral ganglion. The fact that so many stages in the development of these neuroblasts are shown in the ganglia found along the maxillary nerve (Pl. II. Fig. 7 ) seems to favor such a view.

The sphenopalatine ganglion of the adult fowl is more or less like a chain of small ganglia on the maxillary nerve. On the persistant branch of this nerve of the eleven day chick embryo is a similar chain of ganglia. It may therefore be concluded, that this branch of the maxillary nerve is probably identical with the one in the adult fowl on which the sphenopalatine ganglion is found, and that its chain of ganglia is very possibly the embryonic sphenopalatine ganglion.



## IV. SUMMARY.

1. The periax<sup>i</sup>al cords, resulting from the proliferation and condensation of cells derived from the neural crest in the region of the mandibular and hyoid arches, are the primordia of the Gasserian and the acustico-facialis ganglia, and mark the paths of the trigeminal and facial nerves (Lillie, The Development of the Chick).

2. The development of the ophthalmic branch is considerably in advance of the maxillo-mandibular branch in the earliest embryonic stages of the chick.

3. In embryos of about seven days' incubation the maxillo-mandibular nerve has more branches than in the earlier or in the later stages.

4. At the stage of about nine days' incubation, peripheral ganglia have developed on the maxillary and mandibular nerves. There is a more or less scattered group of ganglia on two branches of the maxillary nerve, and a single elongated ganglion on one branch of the mandibular nerve.

5. After ten days and five hours' incubation we find an apparently isolated nerve (except for a possible connection across the median plane of the head) in the upper mandible. It lies close to the median plane and has several small ganglia scattered along its course.

6. The characteristic features of the maxillo-mandibular division of the trigeminal nerve of an eleven day chick embryo are as follows: First, a completely isolated and



apparently disintegrating nerve in the upper mandible near the median plane; on this nerve are scattered ganglia, the cells of which show signs of disintegration. Second, a somewhat scattered group of ganglia on a branch of the maxillary nerve; this group of ganglia probably makes up the indefinite sphenopalatine. Third, a single elongated ganglion, possibly the submaxillary, near the distal end of a branch of the mandibular nerve. Fourth, a few very small and scattered ganglia on one of the branches of the maxillary nerve which belong to the orbital group.

7. The cells of the adult sphenopalatine ganglion are scattered and the boundary of the ganglion is therefore difficult to determine.





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## VI. EXPLANATION OF PLATES.

All the figures are drawn from preparations of chick embryos. In figures 1, 2, 3 and 5 the nerve is a graphic reconstruction from the entire series of sections. In figures 1 to 3 inclusive the land marks are camera lucida drawings from lateral sagittal sections. Figures 4, and 6 to 9 inclusive are camera lucida drawings.

### List of Abbreviations.

cl. gn. cil.....	Ganglion cells of ciliary ganglion.
cl. gn. Gas.....	Ganglion cells of Gasserian ganglion.
cl. gn. mx.....	Ganglion cells of peripheral ganglia. on maxillary branch of trigeminus.
cl. gn. sph.....	Ganglion cells of sphenopalatine ganglion.
cl. gn. trans.....	Ganglion cells of ganglia on isolated nerve in upper mandible of chick embryo.
crt. Mk.....	Meckel's cartilage.
gn. Gas.....	Gasserian ganglion.
gn. md.....	Ganglion on mandibular branch of trigeminus.
gn. mx.....	Ganglion on maxillary branch of trigeminus.
gn. sph.....	Sphenopalatine ganglion.
mth.....	Mouth.
mu. rt. e.....	External rectus muscle.



mx. orb. 1, 2 ..... Orbital branch of maxillary nerve.  
 n. abd. .... Abducent nerve.  
 os. qd. .... Quadrate bone.  
 os. sup. al. .... Supra-angular bone.  
 par. mt'e. v. .... Ventral wall of hind-brain.  
 pl. md. .... Median plane of head.  
 rm. md. .... Mandibular branch of trigeminus.  
 rm. mu. rt.e. .... Ramus to external rectus muscle.  
 rm. mx. .... Maxillary branch of trigeminus.  
 rm. opth. .... Ophthalmic branch of trigeminus.  
 v. in'pl. .... Infrapalatine vein.



## P L A T E    I

Fig. 1. Land marks from lateral sagittal section of chick embryo of five days' incubation. Nerve reconstructed.

Fig. 2. Land marks from lateral sagittal section of chick embryo of about seven days' incubation. Nerve reconstructed.

I, IIa, IIb..... Rami of the maxillary branch  
of the trigeminus.

1, 2, 3..... Rami of the mandibular branch  
of the trigeminus.

Fig. 3. Land marks from lateral sagittal section of chick embryo of about nine days' incubation. Nerve reconstructed.

I, II..... Rami of the maxillary branch  
of the trigeminus.

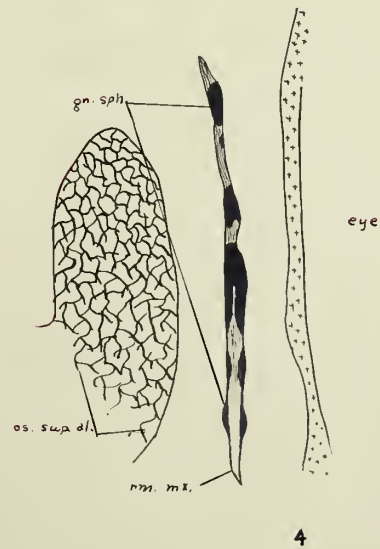
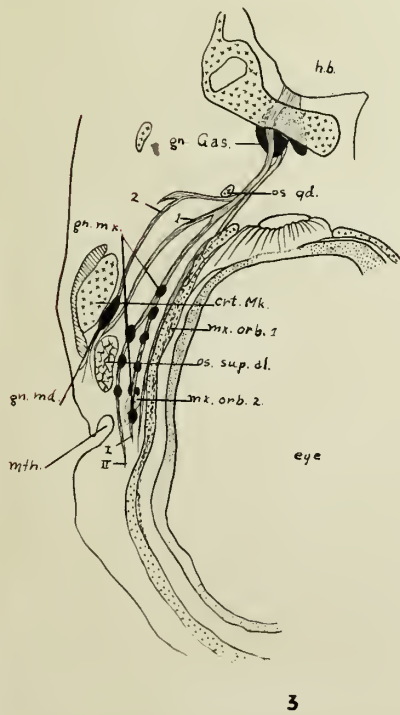
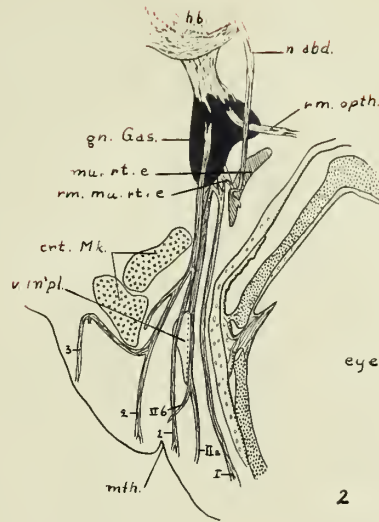
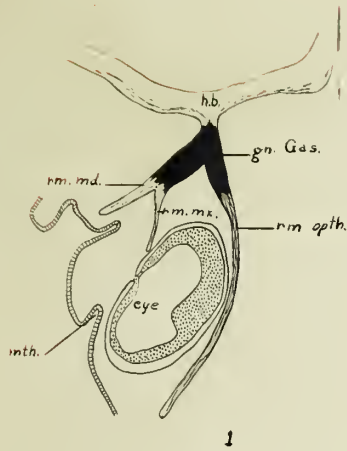
1, 2 ..... Rami of the mandibular branch  
of the trigeminus.

Fig. 4. Part of the maxillary branch showing sphenopalatine ganglion.





# PLATE I.





## P L A T E II.

Fig. 5. Reconstruction of apparently isolated nerve in the upper mandible of a chick embryo of ten days and five hours' incubation.

Fig. 6. Part of isolated nerve in upper mandible of chick embryo of eleven days and one hours' incubation x 150.

Fig. 7. Part of the series of ganglia found on the maxillary branch of the trigeminus in a chick embryo of about nine days' incubation x 900.

Fig. 8. Two groups of neuroblasts drawn from sections of a chick embryo of eleven days and one hour's incubation x 1500.

Fig. 9. Three groups of ganglia drawn from the ciliary, Gasserian and maxillary ganglia respectively, of a chick embryo of about nine days' incubation x 1500.





# PLATE II.



5



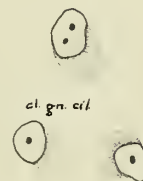
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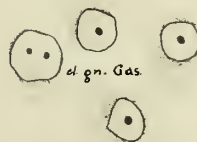
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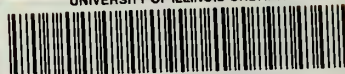








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